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PHYTOLOGIA

An international journal to expedite plant systematic, phytogeographical and ecological publication

Vol. 84 May 1998 No. 5

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A NEW SPECIES OF *WEDELIA* FROM ECUADOR (HELIANTHEAE: ASTERACEAE)

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ABSTRACT

Wedelia loxensis is described as a new species.

KEY WORDS: Asteraceae, Heliantheae, *Wedelia loxensis*, Ecuador

The following new species has been discovered during preparation of the treatment of the Heliantheae for the Flora of Ecuador. The material has been held for some time with the hope of finding more collections, but as yet no additional specimens have been seen, and validation is needed. The description is as follows.

Wedelia loxensis H. Rob., *spec. nov.* TYPE: ECUADOR. Loja, between Celica and El Empalme on the Catacocha-Macará road, 1-2 km above El Empalme, 800-1000 m, 11 Apr 1980, *Harling & Andersson 18174* (HOLOTYPE: US; Isotype: GB).

Plantae suffrutescentes erectae vel procumbentes flexuosae ca. 0.4 m altae; caules flavo-virides vel rubrotincti teretes striati hispidi, pilis rigidis; internodi basilares breves, distales ad 11 cm longi. Folia plerumque opposita sessilia; laminae tenuiter herbaceae oblongo-ovatae vel obovatae plerumque 3-6 cm longae, 2.5-3.0 cm latae, base rotundatae, margine praeter basam minute serrulatae, apice breviter acutae, supra strigillosae pauce glandulo-punctatae subtus leniter pallidiores distincte glandulo-punctatae; nervis secundariis pinnatis ad angula ca. 45° patentibus. Inflorescentiae plerumque trifidae in pedunculis terminales et in ramis aut pedunculis binis lateralibus proliferatae, pedunculis elongatis 10-14 cm longis albo-puberulis et minute contorte pilosulis et pauce minute glandulo-punctatis. Capitula late campanulata vel hemisphaerica 1.0-1.3 cm alta; involucra 1.7-2.0 cm lata, bracteis exterioribus ca. 8 herbaceis ellipticis, plerumque 8-12 mm longis, 3-4 mm latis, interne et externe strigillosis pauce glandulo-punctatis, bracteis interioribus ca. 12

scariosis flavescentibus oblongo-ellipticis, ca. 6 mm longis, 1.5 mm latis, apiculatis, externe sparce pilosulis margine superne denticulatis et ciliatis; paleae ad bracteas interiores similae flavescentes anguste oblanceolatae ca. 7 mm longae in costis pilosulae, laminis a mediis ca. 0.6 mm latis. Flores radii ca. 12 feminei; corollae flavae, tubis ca. 1.5 mm longis pilosulus, limbis anguste oblongis, ca. 13 mm longis, 2.5 mm latis, apice breviter bilobatis subtus glandulo-punctatis. Flores disci 35-45; corollae flavae ca. 5.5 mm longae, tubis ca. 1.5 mm longis glabris, faucibus ca. 3 mm longis fere glabris, lobis ca. 0.7 mm longis, 0.5 mm latis, extus puberulis et glandulo-punctatis; thecae antherarum 2 mm longae; appendices apicales pallidae extus pauce glanduliferae. Cypselae (submaturae) ca. 2.5 mm longae, puberulae in vel prope rostris glandulo-punctatae, rostris ca. 0.4 mm longis; pappus minime coroniformis margine glanduliferis et leniter lobatis.

Wedelia loxensis is known only from the type collection. It was collected in a deciduous–forest at 800-1000 m elevation in western Loja, Ecuador. It is easily distinguished from other Andean species with fertile rays by its sessile leaves with ascending, pinnate venation.

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NEW SPECIES AND NEW COMBINATIONS OF NEOTROPICAL EUPATORIEAE (ASTERACEAE)

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ABSTRACT

Gongrostylus pipolyi, ***Guevaria micranthera***, ***Hebeclinium palaciosii***, and three species of *Ophryosporus*, ***Ophryosporus carchiensis***, ***O. ferreyrii***, and ***O. sagasteguii*** are named as new. New combinations are provided for *Eupatorium constanzae*, *E. diversifolium*, and *E. haageanum* in *Koanophyllon*, *Fleischmannia*, and *Ageratina* respectively.

KEY WORDS: Asteraceae, Eupatorieae, Neotropics, *Gongrostylus*, *Guevaria*, *Ophryosporus*, *Koanophyllon*, *Fleischmannia*, *Ageratina*, *Eupatorium*

A number of separate studies, including work on the Eupatorieae for the Flora of Ecuador, have shown the need for the description of the following new species and new combinations. The needs in *Ophryosporus* are particularly notable, with one new species showing an intermediate condition between the pappose and epappose states that are present in that genus.

NEW COMBINATIONS

Ageratina haageana (Regel & Koern.) H. Rob., *comb. nov.* BASIONYM: *Eupatorium haageanum* Regel & Koern., *Ind. Sem. Hort. Petrop.* 40. 1857. Probable type material has been seen from Vienna (W), and it is an *Ageratina* rather similar to *A. pazcuarensis* (H.B.K.) R.M. King & H. Rob. but with leaves more laciniately toothed and more strongly acuminate. The material might be a horticultural variant.

Fleischmannia diversifolia (Schrad.) H. Rob., *comb. nov.* BASIONYM: *Eupatorium diversifolium* Schrad., *Ind. Sem. Hort. Acad. Gott.* 1134. 1829. The name was placed in the synonymy of *Fleischmannia pycnocephala* (Less.) R.M. King & H. Rob. by King & Robinson (1987), but the Schrader name is the older name and would take priority.

Koanophyllon constanzae (Urban) H. Rob., *comb. nov.* BASIONYM: *Eupatorium constanzae* Urban, *Symb. Antill.* 7:422. 1912. Type material has been seen, and it represents a distinct, rather narrow-leaved, species of *Koanophyllon* from the Dominican Republic.

Type material from Vienna (W) has also been seen of *Eupatorium myosotifolium* Jacq. and it proves to be a synonym of *Cyanthillium cinereum* (L.) H. Rob. of the Vernonieae.

NEW SPECIES

Guevaria micranthera H. Rob., *spec. nov.* TYPE: PERU. Amazonas: along road ascending mountain SE of Chachapoyas, ca. 9000 ft., Creeping herb on moss-covered rock, 14 Jan 1983, *King & Bishop 9199* (HOLOTYPE: US; Isotype: MO). Paratype: PERU. Amazonas: 28 kms along road from Leimebamba SW towards Celendín, ca. 9700 ft., 19 Jan 1983, *King & Bishop 9251* (MO,US).

In tubis corollarum brevibus et in antherae minutae distincta.

Decumbent perennials to 1.5 dm high, with spreading branches and long rhizomes; stems hirsute with whitish hairs, apparently not fistulose. Leaves opposite; petioles 2-3 mm long; blades ovate, often thin and very translucent, 7-12 mm long, 4-9 mm wide, base very broadly obtuse, subtruncate, margins crenulate-serrate, 5 or 6 teeth on each side, apex short-acute, densely pilose on both surfaces, with sparse glandular dots below. Inflorescences borne erect, raised on long internodes, strongly cymose, usually with 3 or 9 heads; peduncles slender, mostly 5-15 mm long, puberulous with small, ascending pale hairs. Heads 2.5-3.0 mm high, to 4.5 mm wide; involucral bracts ca. 14 in ca. 2 series, rather obovate, ca. 2 mm long, apex thin, rounded, subscarious near margins and tips, ciliate with small hairs, with few hairs outside distally, otherwise glabrous. Florets ca. 40-50 in a head; corollas white, ca. 1 mm long, tube ca. 0.3 mm long, broad at base with spreading, tapering, uniseriate hairs, tube strongly constricted above with few short-stalked glands; throat abruptly and widely ampliate, ca. 0.4 mm long, ca. 0.9 mm wide, with very few nearly sessile glands; lobes ca. 0.3 mm long, densely papillose inside, outside with few glandular dots below, numerous, short, moniliform hairs nearer tip, with numerous small papillae at tip; anther thecae ca. 0.25 mm long. Cypselas ca. 1.2 mm long, oblong, glabrous, contracted below to short pale carpopodium.

Guevaria micranthera is evidently most closely related to opposite-leaved members of the genus farther north in Ecuador, and differs from the previously known species from farther south in Perú, *G. vargasii* (I.C. Chung) R.M. King & H. Rob., which has alternate leaves. The new species has the small-leaved spreading habit closest to the most northern of species of the genus, *G. sodiroi* (Hieron.) R.M. King & H. Rob. The new species is primarily distinguished by details of its florets. The corolla tube is distinctly shorter than the throat, the tube bears only short-stalked glands and the anthers are very small.

Gongrostylus pipolyi H. Rob., *spec. nov.* TYPE: COLOMBIA. Antioquia: Mpio. de Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, sitio La Gurrucha, 06° 32′ N, 76° 19′ W, 700-900 m, 5 Feb 1995, *Pipoly et al. 18406* (HOLOTYPE: JAUM; Isotypes: MO,US). Paratype: COLOMBIA. Chocó, Río San Juan just below Tadó, ca. 100 m, 15 Aug 1976, *Gentry & Fallen 17725* (COL,MO,US).

A *Gongrostylo costaricense* (O. Kuntze) R.M. King & H. Rob. in foliis breviter acutis et in setis pappi apice minute latiores distinctus.

Somewhat woody, scandent, slender epiphyte with few branches, branches spreading at 45°-80° angles; stems densely pilose to hirsutulous with blackish hairs. Leaves opposite; petioles 5-11 mm long; blades ovate, 2.5-6.5 cm long, mostly 1.3-3.0 cm wide, shortly acute, surfaces sparsely pilosulous, mostly on veins below, trinervate 3-8 mm above base, with veins parallel to margin in basal half. Inflorescence narrowly pyramidally thyrsoid with lateral branches from axils of leafy bracts, branches densely puberulous with dark hairs; peduncles 0.5-2.3 cm long. Heads 8-10 mm high; involucral bracts ca. 25, subimbricate in ca. 3 series, oblong-ovate to lanceolate, 3.5-7.0 mm long, mostly 1.0-1.8 mm wide, shortly to narrowly acute, glabrous outside, outer bracts thicker and darker, inner bracts paler and striated; receptacle glabrous. Florets ca. 90 in a head; corollas whitish, narrowly funnelform, 6.0-6.5 mm long, glabrous outside below lobes, with scattered uniseriate hairs inside tube and lower throat, tube ca. 3 mm long, throat ca. 3 mm long, lobes ca. 0.5 mm long, with few glandular dots on outer surface; anther thecae ca. 1 mm long, apical appendage very short and broad; style base enlarged, densely hirsute; tips of style branches greatly enlarged. Cypselas ca. 2.2 mm long, glabrous; carpopodium with enlarged basal row of cells; pappus of ca. 30 slender bristles up to 5.5 mm long, longer bristles with slightly but distinctly broadened tips and with rounded apical cells.

Gongrostylus pipolyi is apparently a local endemic in the Pacific coastal area of Colombia. It is a second described species of a previously unispecific genus. It differs from the more widely distributed *G. costaricensis* (O. Kuntze) R.M. King & H. Rob. by the shortly acute rather than narrowly acuminate leaves and the slightly enlarged tips of the longer pappus bristles with rounded apical cells. The hairs on the inside of the corollas are easily overlooked, but apparently occur in both species.

Hebeclinium palaciosii H. Rob., *spec. nov.* TYPE: ECUADOR. Zamora-Chinchipe: Nangaritza Cantón Pachicutza, camino al Hito, 04° 07′ S, 78° 37′ W, 900 m, 18 Oct 1991, *Palacios, Aymard, & Frieire 8265* (HOLOTYPE: US; Isotypes: MO,QCNE).

Ad *Hebeclinio bullatissimo* (B.L. Rob.) R.M. King & H. Rob. similis sed in caulibus lanulatum in marginibus foliorum serratum in receptaculis sparse hirsutum et in floribus 12-15 in capitulo distinctum.

Weak shrub to 1 m high, sparingly branched; stems terete, brownish lanulate. Leaves opposite; petioles 1.5-4.0 cm long; blades ovate, chartaceous, 4-11 cm long, 2.0-5.5 cm wide, base broadly obtuse to rounded, margins closely serrate, apex acute to scarcely acuminate, upper surface slightly bullate, sparsely pilose with weak hairs, lower surface hirtellous mostly on veins, without evident glandular dots; venation pinnate with ca. 4 ascending secondary veins on each side. Inflorescence a small terminal pyramidal panicle, branches lanulate, cymose, ending in small clusters of heads; peduncles 1-3 mm long, tomentellous. Heads ca. 6 mm high; involucral bracts ca. 35 in ca. 5 series, orbicular to narrowly oblong, 1-4 mm long, 0.7-1.0 mm wide, apices rounded, outer surface glabrous with 3 green lines; receptacle sparsely hirsute. Florets 12-15 in a head; corollas narrowly funnelform, white, ca. 2.8 mm long, glabrous outside below lobes, tube ca. 1 mm long, throat ca. 1.2 mm long, with long hairs inside, lobes ca. 0.3 mm long, with hairs and glandular dots outside; anther thecae ca. 1 mm long; style appendages filiform. Cypselas ca. 1.5 mm long, nearly glabrous, with 1 or a few small setulae above; pappus of ca. 35 white bristles to 2.8 mm long, longer bristles somewhat broadened distally.

The species is known only from the type collection. The specimen was stated to be on a rock in a very shaded place. The species is closely related to *Hebeclinium bullatissimum* (B.L. Rob.) R.M. King & H. Rob. from Ecuador and northern Perú, but the latter has consistently appressed minute puberulence on the stems, crenulate or crenate leaf margins, a glabrous receptacle and 22-30 florets in a head.

Ophryosporus carchiensis H. Rob., *spec. nov.* TYPE: ECUADOR. Carchi: Cantón Montufar, Loma El Corazón (Bretaña) al SE de Mariscal Sucre, Río Minas, 00° 35′ N, 77° 42′ W, 3150 m, bosque muy húmedo Montano, 22-23 Dec 1992, *Palacios & Tipaz 10524* (HOLOTYPE: US; Isotypes: MO,QCNE).

A *Ophryosporo sodiroi* Hieron. in cypselis setuliferis et in rami stylorum angustioribus distinctus.

Vine with branches spreading at 90° angles; stems brownish, terete, densely puberulous; pith solid. Leaves opposite; petioles 3-8 mm long; blades ovate, 1.8-2.8 cm long, 1.0-1.8 cm wide, base obtuse to short-acute, margins sharply and closely serrate-dentate above widest part, apex acute, upper surface glabrous, lower surface pilose with long hairs mostly crowded along veins, without glandular dots, not viscid, weakly trinervate with ascending secondary veins from well above base. Inflorescence pyramidal to broadly thyrsoid with branches spreading at 90° angles; branches densely pilosulous to tomentellous with brown hairs, peduncles 1-6 mm long, densely pilosulous. Heads 4.5-5.5 mm high; involucral bracts 5 or 6, drying brown, broadly elliptical to obovate, 3.0-3.5 mm long, 1.0-1.5 mm wide, margins thin, subscarious, apex rounded and minutely toothed, outer surface glabrous. Florets 6 or 7 in a head; corollas creamy white, ca. 3 mm long, with narrow-tipped glandular hairs outside on tube and throat, tube ca. 1 mm long, throat broadly funnelform, ca. 1.5 mm long, lobes ca. 0.5 mm long, densely low-papillose inside, with few glands outside; anther thecae ca. 0.8 mm long; tips of style branches slightly broadened. Cypselas ca. 1.7 mm long, mostly glabrous, with few setulae near top; pappus of 20-23 bristles ca. 2.5 mm long, slightly broadened at tips, apical cells with rounded tips.

Ophryosporus carchiensis is known only from the type collection. The species is in the scandent group of the genus which includes *O. sodiroi* Hieron. of southern Ecuador and *O. ovatus* B.L. Rob. of northern Perú. The present species differs by the weaker trinervation and coarser serration of the leaves, the less enlarged tips of the style branches and the apically setuliferous rather than glanduliferous cypselas.

The three specimens of one collection described here as *Ophryosporus carchiensis* were initially determined as *O. serratifolius* (H.B.K.) B.L. Rob. The latter was questionably credited to Colombia, the only member of the genus credited to that country. The type specimen of *O. serratifolius* in Paris was examined by B.L. Robinson, who in 1930 indicated it was unquestionably an *Ophryosporus*. The species has not been recollected from Colombia, and it is doubtfully cited from there. The descriptions of *O. serratifolius* indicate a rather distinctive plant that matches most closely specimens seen in this study from northern Perú (*Ferreyra & Chanco 20436; Llates Quiraz 1199*). The latter collections agree with the original description in having glabrous 6-angled stems, 5 involucral bracts and 5 florets. Most members of the genus have terete stems.

If *Ophryosporus serratifolius* is properly Peruvian, then the new species, *O. carchiensis* is the northernmost known representative of the genus.

Ophryosporus ferreyrii H. Rob., *spec. nov.* TYPE: PERU. Lima: Prov. Huarochirí, Carretera Central, Infiernillo, 3200 m, high montane, semi-arid shrublands, clambering shrub, flowers white, sweet odor, 10 May 1984, *Smith, Ferreyra, & Tovar 7002* (HOLOTYPE: US; Isotypes: MO,USM). Paratypes: PERU. Lima: Huarochirí, abajo del puente de Infiernillo, carretera Lima-Huancayo, 3300-3400 m, pedregoso, sufruticosa, flores blancas, 8 Aug 1949, *Ferreyra 6247* (US,USM); Same locality, arriba de Infiernillo, 3300-3350 m, habitat pedregoso, 0.6-1.0 m, 19 June 1950, *Ferreyra 7706* (US,USM); Central highway 7 km NE of San Mateo on road to La Oroya, shrub to 3 ft., on cliff above road, rays white, 22 June 1966, *Edwin & Schunke 3796* (F,US); Same locality, arriba de San Mateo, falda de cerro, 3200-3400 m, flores blancas, 7 May 1966, *Riccio & La Rosa 554* (US,USM); ca. 4 km E of San Mateo, ca. 117 km E of Lima on road to La Oroya, ± 3600 m, disturbed roadside, shrub to 1.5 m, flowers white, styles white, 7 Jul 1981, *Dillon 2511* (F,MO,US,USM). Prov. Canta, Lachaqui sobre la población, 3800-3900 m, en ladera estepa de gramíneas con arbustos dispersos, flores blancas, 29 June 1992, *Arturo Granda P. 597* (MOL,US).

A *Ophryosporo heptantho* (Sch.-Bip. *ex* Wedd.) R.M. King & H. Rob. in foliis latioribus et argute duplo-serratis distinctus.

Erect to clambering shrubs to 1.5 m high, moderately branched, branches spreading at 60-80° angles; stems pale to dark brown, terete, densely puberulous with brownish hairs; pith solid. Leaves opposite; petioles 0.2-0.8 cm long; blades ovate, mostly 1-5 cm long, 0.7-3.5 cm wide, base broadly obtuse, entire, margins from widest part with large, crowded, jagged, doubly serrate teeth, apex acute, upper surface dark green, pilosulous, lower surface somewhat paler, puberulous mostly on veins, with scattered glandular dots, trinervate with strongly ascending veins near base. Inflorescences corymbiform to subpyramidal, with branches spreading at ca. 90° angles, ending in dense corymbiform clusters of heads; peduncles 1-4 mm long, puberulous. Heads ca. 9 mm high, 2-3 mm wide; involucral bracts ca. 7, green, narrowly oblong to linear, ca. 6 mm long, 1 mm wide, acute at tips, puberulous outside. Florets 6-9 in a head; corollas white, ca. 6 mm long, with scattered glands outside mostly on basal tube and lobes, tube ca. 1 mm long, throat narrowly funnelform, ca. 4 mm long, lobes ca. 1 mm long, 0.5 mm wide, mamillose inside; anther thecae ca. 2 mm long, with small rudimentary appendage; style branches gradually but distinctly broadened at tips. Cypselas ca. 3.5 mm long, with scattered glands on ribs; with slender, pale, crooked stipiform base ca. 0.5 mm long, with firm-walled elongate cells and bearing numerous glands; pappus of ca. 30 irregularly subplumose bristles to 4.5 mm long, not broadened distally, apical cells narrowly acute.

Ophryosporus ferreyrae is evidently a close relative of *O. heptanthus* (Sch.-Bip. *ex* Wedd.) R.M. King & H. Rob., including *O. origanoides* (Meyen & Walp.) Hieron. of central Perú in Junín southward into Bolivia. The latter differs by the more ascending branches and the narrower leaf blades with more rounded bases and only subserrulate to simply serrate margins. Both species have the extended, slender, stipitate base of the cypsela, but the stipe in *O. heptanthus* has thinner-walled cells that are more sharply differentiated from the carpopodium.

Ophryosporus sagasteguii H. Rob., *spec. nov.* TYPE: PERU. Cajamarca: Contumazá, Contumazá-Cascabamba, 2700 m, ladera, 12 June 1981, *Sagástagui, López, & Mostacero 9975* (HOLOTYPE: US; Isotype: HAO).

A *Ophryosporo* cetero in caulis fistulosis et in setis pappi sparsis distinctus.

Subshrub 1-2 m high, moderately branched, with branches diverging at ca. 45° angles; stems brown, terete, sparsely puberulous near nodes, glabrescent, narrowly fistulose. Leaves opposite; petioles 2-8 mm long; blades narrowly ovate, to 3.5 cm long and 1.5 cm wide, base broadly obtuse, margins serrulate to obtusely and somewhat unevenly serrate, with 6-12 teeth on each side, apex acute, upper surface sparsely minutely puberulous, somewhat paler and puberulous mostly on veins below, trinervate from near base. Inflorescence broadly thyrsoid, with central axes of inflorescence and lateral branches usually aborting and forming pseudodichotomies at tips; branches densely puberulous with whitish or sordid hairs; peduncles 0-1 mm long. Heads ca. 4.5 mm high, ca. 2 mm wide; involucral bracts usually 5 in 1-2 series, narrowly oblong, ca. 3.0-3.5 mm long, ca. 0.8 mm wide, apex obtuse to short-acute, sparsely puberulous outside. Florets usually 5 in a head; corollas whitish, tinged with red distally, ca. 3 mm long, with numerous narrow-tipped stalked glands outside on tube, throat and lobes, tube ca. 1 mm long, throat cylindrical, ca. 1.5 mm long, lobes ca. 0.5 mm long, smooth inside; anther thecae ca. 1.5 mm long; tips of style branches distinctly enlarged. Cypselas (immature) ca. 1 mm long, with numerous setulae near top and bottom, glabrous between; carpopodium shortly stopper-shaped; pappus usually with 4-14 bristles, sometimes totally lacking, with irregular scabrae or barbules.

Ophryosporus sagasteguii is evidently very limited in distribution in southern Cajamarca, an area where many members of the genus occur. The variation in the pappus nicely bridges the now abandoned distinction between *Ophryosporus* and the old concept of *Piqueria* sect. *Artemisioides*. The species may be of hybrid origin, but it possesses at least one other distinctive feature that has been seen in no potential parent, a narrowly fistulose stem. The slightly reddish apices of the corollas also seem somewhat distinctive.

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INVESTIGATION OF THE WOOD ANATOMY OF *JUNIPERUS* (CUPRESSACEAE) FOR TAXONOMIC UTILIZATION

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ABSTRACT

The wood anatomy of twenty three taxa of *Juniperus* of the Western Hemisphere was analyzed and data presented for rays/mm, growth ring size, ray cell height, tracheid lumen size, tracheid wall thickness, and tracheid pit and border diameter. The genus was found to be very homogenous in its wood anatomy. Species differed only quantitatively and could not be separated due to overlapping ranges for these data. The wood anatomical characters examined were not useful for taxonomic purposes at the species level in *Juniperus*.

KEY WORDS: Cupressaceae, *Juniperus*, wood anatomy

The *Juniperus* species of the Western Hemisphere include approximately 43 taxa. They may be divided into several groups based on morphology (Zanoni & Adams 1978; Adams 1995) and DNA (Adams 1994; Adams & Demeke 1993):

Section *Juniperus* (acicular leaves, articulated at the base):
  J. communis L. var. *saxatilis* Pall. and var. *depressa* Pursh
Section *Sabina* (scale like and decurrent leaves, not articulated at the base) (see serrate and smooth leaves below):
  Serrate leaves (most taxa are associated with arid lands):
    J. angosturana R.P. Adams (= *J. monosperma* (Engelm.) Sarg. var. *gracilis* Mart.); *J. ashei* Buch.; *J. californica* Carr.; *J. coahuilensis* (Mart.) Gaussen *ex* R.P. Adams var. *coahuilensis* (= *J. erythrocarpa* Cory, in part, see

Adams 1994) and var. *arizonica* R.P. Adams; *J. comitana* Mart.; *J. deppeana* Steudel var. *deppeana* and f. *sperryi* (Correll) R.P. Adams and var. *pationana* (Mart.) Zanoni; var. *robusta* Mart., and var. *zacatacensis* Mart., *J. durangensis* Mart.; *J. flaccida* Schlecht. var. *flaccida*, var. *martinezii* (Perez de la Rosa) Silba, and var. *poblana* Mart.; *J. gamboana* Mart., *J. jaliscana* Mart., *J. monosperma* (Engelm.) Sarg.; *J. monticola* Mart. f. *compacta* Mart., f. *monticola*, and f. *orizabensis* Mart.; *J. occidentalis* Hook. var. *australis* (Vasek) A.H. & N.H. Holmgr. and var. *occidentalis*; *J. osteosperma* (Torr.) Little; *J. pinchotii* Sudw.; *J. saltillensis* M.T. Hall; and *J. standleyi* Steyerm.

The entire (or smooth) leaf margined junipers are mostly associated with more mesic habits or mountains. These junipers can be divided into the mainland and Caribbean Island species (Adams 1995):

Smooth leaves, Mainland:

J. blancoi Mart.; *J. horizontalis* Moench; *J. scopulorum* Sarg. and *J. virginiana* L. var. *virginiana* and var. *silicicola* (Small) E. Murray.

Smooth leaves, Caribbean Islands:

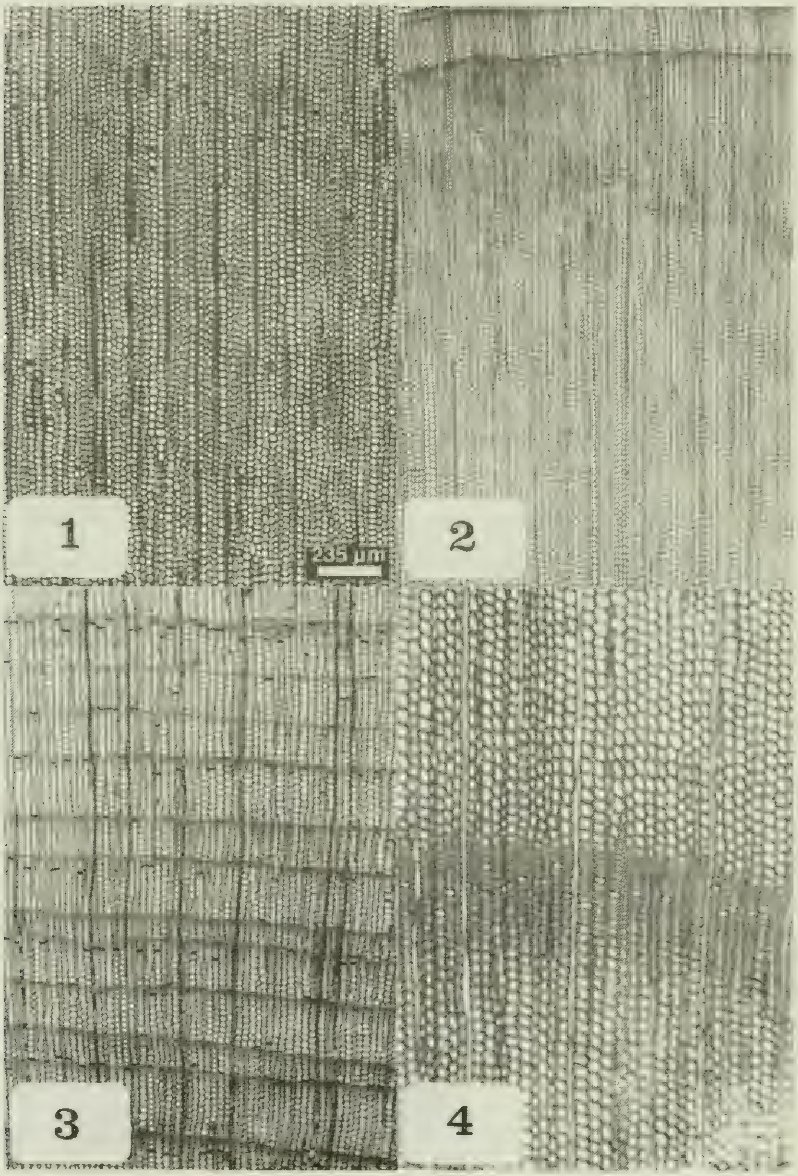
J. barbadensis L.; *J. bermudiana* L.; *J. gracilior* Pilger var. *gracilior*, var. *ekmanii* (Florin) R.P. Adams, and var. *urbaniana* (Pilger & Ekman) R.P. Adams; *J. lucayana* Britton; *J. saxicola* Britt. & P. Wilson.

The wood of the timber-producing members of the family share the following features: latewood never conspicuous, alternate bordered pits of the tracheids lacking, tracheids without spiral thickenings, parenchyma present and frequently abundant, cupressoid (Pierce 1937) cross-field pits present, except in *Thuja*, and resin ducts lacking.

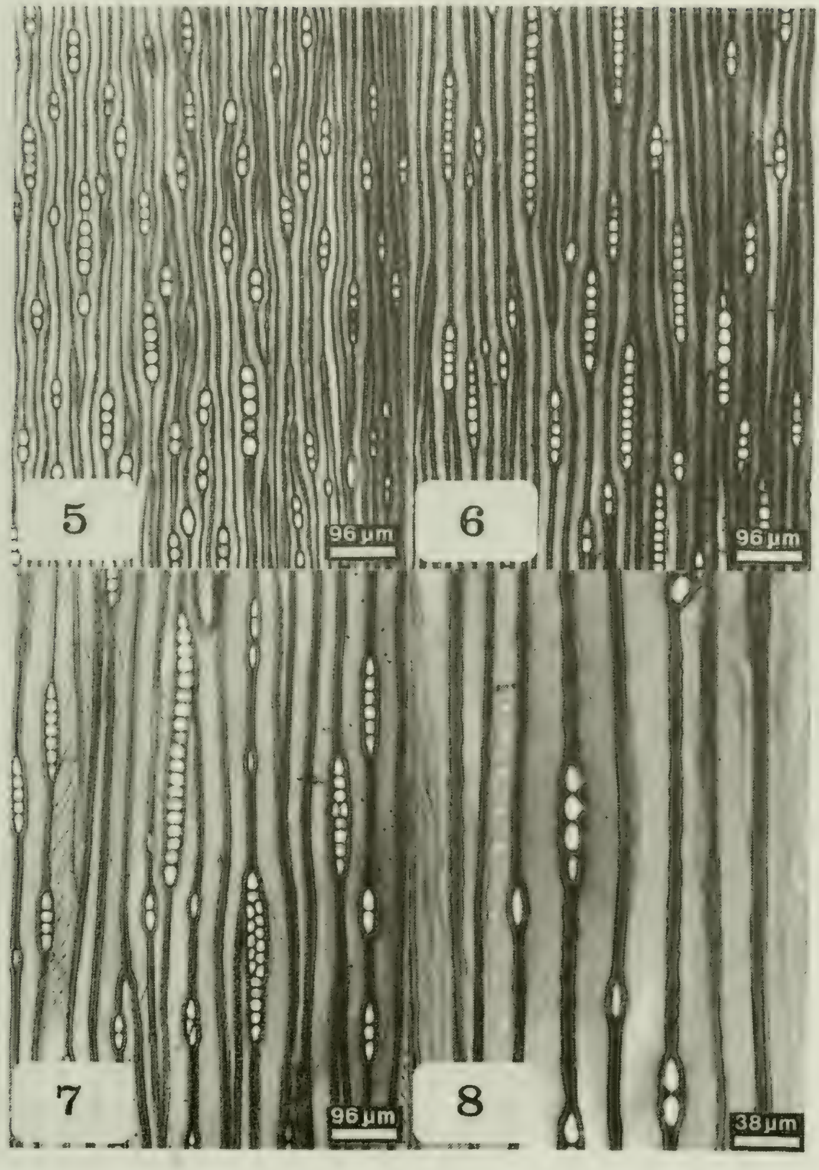
Many species of *Juniperus* are readily distinguished from all other conifers (except *Cupressus* and *Cedrus*) by the peculiar cedar-like odor which one normally associates with pencils. In fact, the cedarwood oil is practically identical for *Juniperus ashei*, *J. virginiana*, and *Cupressus funebris* Endl. (Adams 1991). Anatomically, these species are separated from most other gymnosperm woods by the presence of abundant parenchyma with nodular transverse walls and the cupressoid cross field pits.

Phillips (1968) and Panshin & de Zeeuw (1964) reported that *Juniperus virginiana* and *J. lucayana* differ from other *Juniperus* species by the presence of nodular thickenings on the vertical end walls of the rays. Nevertheless, according to Jacquiot (1955), the wood structure of the genus *Juniperus* is very homogeneous and the differences between the various species are mostly biometrical.

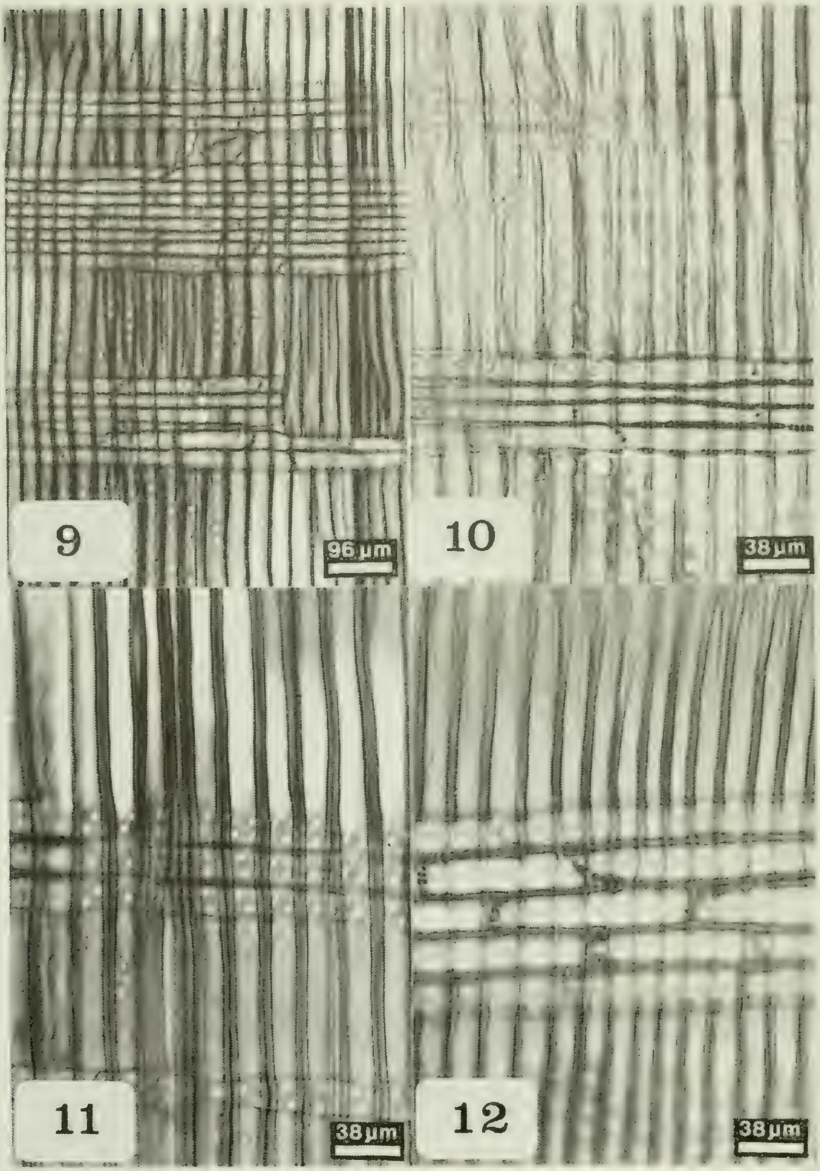
A systematic examination of the wood anatomy of the *Juniperus* from the Western Hemisphere has not been reported. The present research was an exploratory effort to evaluate the taxonomic utility of wood anatomy using a large portion of the *Juniperus* species (section *Sabina*) in the Western Hemisphere.



Figures 1-4. Transverse sections. 1. *Juniperus monosperma* (*Adams 6884*) México; 2. *J. saxicola* (*Adams 5284*) Cuba. 3. *J. barbadensis* (*Adams 5368*) St. Lucia: 4. *J. monticola* f. *monticola* (*Adams 6874*) México.



Figures 5-8. Tangential sections. 5. *Juniperus saltillensis* (*Adams 6886*); 6. *J. deppeana* var. *zacatacensis* (*Adams 6840*); 7. *J. gracilior* var. *ekmanii* (*Adams 3107*); 8. *J. barbadensis* (*Adams 5368*).



Figures 9-12. Radial sections. 9. *Juniperus gamboana* (*Adams 6864*); 10. *J. saxicola* (*Adams 5284*); 11. *J. barbadensis* (*Adams 5368*); 12. *J. monticola* f. *monticola* (*Adams 6874*).

WOOD SAMPLES

Wood samples were obtained from the following taxa: (species, herbarium voucher number, location): *Juniperus angosturana, Adams 6884*, México; *J. ashei, Adams 5105*, U.S.A. (Texas); *J. barbadensis, Adams 5368*, St. Lucia; *J. blancoi, Adams 6849*, México; *J. coahuilensis, Adams 4988*, U.S.A. (Texas); *J. comitana, Adams 6862*, border México-Guatemala; *J. deppeana* var. *patoniana, Adams 6838*, México; *J. deppeana* var. *robusta, Adams 6825*, México; *J. deppeana* var. *zacatacensis, Adams 6840*, México; *J. durangensis, Adams 6832*, México; *J. ekmanii, Adams 3107*, Haiti and *Adams 5243*, Dominican Republic; *J. flaccida* var. *flaccida, Adams 6892*, México; *J. flaccida* var. *poblana, Adams 6871*, México; *J. gamboana, Adams 6864*, border México-Guatemala; *J. gracilor, Adams 5242*, Dominican Republic; *J. jaliscana, Adams 6846*, Mexico; *J. lucayana, Adams 5280*, Cuba; *J. monosperma, Adams 5027*, U.S.A. (Texas); *J. monticola* f. *compacta, Adams 6898*, México; *J. monticola* f. *monticola, Adams 6874*, México; *J. pinchotii, Adams 5006*, U.S.A. (Texas); *J. saxicola, Adams 5284*, Cuba; *J. scopulorum, Adams 4973*, U.S.A. (Utah). All vouchers are at SRCG.

METHODS

Transverse, radial, and tangential sections were cut at 20-30 µm thickness on a sledge microtome. All slides were stained with Safranin. Averages were based on 25 randomly selected measurements. The IAWA list of microscopic features (IAWA Committee 1989) was used for some of the methodology.

RESULTS

The wood anatomy of *Juniperus* of the Western Hemisphere has the following characteristics (see Table 1 and Figs. 1-12):

Growth rings: Distinct, as a result of a marked contrast between the final rows of the latewood tracheids and the succeeding rows of the earlywood tracheids. The number of growth rings per mm is very variable, from 0.1 up to 5.5, commonly between 0.6 and 1.5 (Table 1).

Table 1. Summary of the wood anatomy for some *Juniperus* of the Western Hemisphere.

Species	Rays/ mm	Growth rings/ mm	Ray height cells	Lumen (µm)	Wall (µm)	Pit diameter (µm) pit/border
Serrate leaves:						
J. angosturana	7(5-8)	0.1	1-10	29	3	4-5/10-13
J. ashei	7(4-8)	2.5	1-5(-6)	16	4	2-3/13-16
J. coahuilensis	7(6-9)	1.5	1-6(-7)	18	3	3/10-11
J. comitana	5-6	1.2	1-7(-9)	21	2-3	5/13
J. deppeana						
var. *patoniana*	8(7-9)	1.4	1-6	17	2-3	3/13
var. *robusta*	6(5-7)	0.75	1-11	28	3	3-4/11
var. *zacatacensis*	6(5-6)	1.2	1-12(-18)	21	2-3	2-3/10-11
J. durangensis	5(4-6)	1.6	1-5(-8)	23	2-3	3-5/13
J. flaccida						
var. *flaccida*	6(5-8)	0.7	1-6(-7)	18	3	3-5/10-11
var. *poblana*	5	1.5	1-5(-9)	26	3	3-4/13
J. gamboana	5-6	1.3	1-11	26	3	3-4/16
J. jaliscana	7-8	2.3	1-12	28	4	3-4/13
J. monosperma	7(6-9)	4.3	1-9(-14)	13	2	4/11
J. monticola						
f. *compacta*	7(6-9)	3.1	1-9(-11)	14	3	4/11
f. *monticola*	9(8-11)	0.6	1-9	16	3	4/11
J. saltillensis	9(7-11)	0.6	1-6(-7)	16	3	4/11
Smooth leaves:						
J. barbadensis	5	5.5	1-7	19	3	2-3/11
J. blancoi	6(4-8)	1.0	1-8(-16)	21	4	4-5/13
J. gracilior	4-5(3-6)	1.1	1-8(-9)	26	4	3/10-11
var. *ekmanii (5243)*	4(4-5)	1.5	1-8(-11)	19	3-4	3-4/10-11
var. *ekmanii (3107)*	6(5-7)	N.O.	1-20(-27)	40	3-4	5/10-13
J. lucayana	5(3-7)	2.8	1-4(-5)	18	3	3/11
J. saxicola	6(5-7)	2.0	1-4(-6)	24	3	3/10-13
J. scopulorum	8-9	2.9	1-8(-10)	18	3	3/10-13

N.O. = not observable.

Tracheids: Uniseriate rows of bordered pits (or rarely paired on the radial walls) are present on the radial walls of the earlywood and on both radial and tangential walls of the latewood. Pit apertures 2-4(-5) µm in diameter, the pits 10-13(-16) µm in diameter. Intercellular spaces well-marked as observed in the transverse sections. Maximum lumen diameter between 13 and 21 µm, very occasionally up to 40 µm, walls 2-4 µm. Length 1471-2356 (1205-2793) µm.

Rays: Homogeneous, composed of procumbent cells, 4-9 (3-11) per mm. Generally uniseriate, occasionally also some biseriate. Maximum number of cells rarely over 10, but in a few samples the highest rays up to 18-27 cells. However, the majority of the rays usually 1-4 cells in height.

Horizontal walls fairly thin to thick, sparsely pitted with large elliptical pits. End walls fairly thin to thick, well pitted.

Cross field pits cupressoid, (1-)2-4(-5) per cross field. These pits are regularly arranged, and sometimes show a tendency towards the taxoid type.

Parenchyma: Usually abundant throughout the growth ring, often arranged in tangential zones. Horizontal and tangential walls pitted, often nodular.

DISCUSSION

Nodular end wall thickenings were present in most cells in the *Juniperus* species of this study. It appears that this character can be used to separate *Juniperus* from other genera of the Cupressaceae. Thus, one can separate species of *Juniperus*, anatomically, from most other gymnosperm woods by the presence of abundant parenchyma with nodular transverse walls and the combination of at least some nodular vertical end walls in the rays and medium size cupressoid cross field pits.

The wood anatomy of *Juniperus* of the Western Hemisphere was found to be very homogeneous and differences were entirely quantitative (in agreement with Jacquiot 1955) with respect to the characters included in this study (Table 1). These differences cannot be used to separate species, as the variation within species was larger than between species.

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VALIDATION OF NEW SUPRAGENERIC NAMES IN PINOPHYTA

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ABSTRACT

The long-used class name, **Taxopsida**, is validated and the class name **Podocarpopsida** and subclass **Podocarpidae** are proposed as new. The monogeneric family **Saxegothaeaceae** is validated and segregated into its own, new order **Saxegothaeales**. The order is expanded to include a new monogeneric family **Microcachrydaceae** based on the endemic Tasmanian genus *Microcachrys*.

KEY WORDS: Pinophyta, Microcachrydaceae, Podocarpopsida, Podocarpidae, Saxegothaeaceae, Saxegothaeales, Taxopsida, nomenclature, gymnosperms, Podocarpaceae

In a forthcoming book by Doweld, *Reproductive Morphology of Seed Plants*, several new suprageneric names in Pinophyta Cronq., Takht., et Zimmerm. *ex* Reveal, are required for a modified system of classification of the division based on new studies and data compiled on the morphology and anatomy of the male and female reproductive structures. Two previously suggested but invalidly published names, Taxopsida and Saxegothaeaceae, are validated herein and attributed to the first person to have suggested the name. A new class and subclass, based on the widespread genus *Podocarpus* L'Hér. *ex* Pers., are proposed as coordinate taxa for the new proposed Taxopsida and the already established Pinidae Cronq., Takht.. et Zimmerm. and Taxidae Ehrend. *ex* Reveal. In addition to Saxegothaeaceae, we establish the family Microcachrydaceae and place both in a new order, Saxegothaeales. We note that Farjon & Mill (1999) have proposed conservation of the orthography *Saxegothaea* over Lindley's original *Saxe-Gothaea*. The proposal may not be necessary as Art. 60, Prop. HH (Greuter & Hawksworth 1999), if approved at the next Botanical Congress, will alter automatically the orthography of *Saxe-Gothaea* to *Saxegothaea*. We are using Saxegothaeales, Saxegothaeaceae, and *Saxegothaea* in anticipation of adoption of one of these proposals following Rec. 14A of the *International Code of Botanical Nomenclature* (Greuter *et al.* 1994).

In adopting Gaussen's (1979: p.6) concept that the conifers (his "Coniferae") consist of three distinct "megaphyla" or "ensembles" (his "Pinodines," "Taxines," and "Podocarpines"), we establish the two new classes, Taxopsida and Podocarpopsida, in accordance with the rules and ranks established by the *International Code of Botanical Nomenclature* (Greuter *et al.* 1994). Taxopsida (originally suggested by Florin [1944, 1948a, 1948b, as "Taxales" or "Taxineae"], Pilger & Melchior [1954] and Pant [1959] - all invalidly published [Art. 32.1(c), 36.1]) with arillate seeds represents a distinct taxon within gymnospermous seed evolution, being rooted among the extinct cupular pteridosperms (Lyginopteridophyta). The origin of the Podocarpopsida with their peculiar epimatial structures around the seed is thought to be among the extinct cone-bearing Walchiaceae-Voltziaceae assemblages, having a detached, but common origin with the extant Pinopsida Burnett (*e.g.*, Araucariaceae of Pinopsida is linked to Saxegothaeales of Podocarpopsida by their strobilar structures). The problems associated with the origins and phylogenetic interrelationships of the three classes of Pinophyta will be addressed more extensively in Doweld's new book.

The family name Saxegothaeaceae, originally suggested but not validated by Gaussen (1974a, 1974b, 1976), is validated to accommodate the Chilean genus *Saxegothaea* Lindl. The new family differs from the remainder of Podocarpaceae (excluding the anomalous Tasmanian genus *Microcachrys* Hook.*f.*) by their taxaceous habit, cone-like aggregations of female strobili and amentaceous male strobili, and other characters as noted by Gaussen. It is noteworthy that in proposing the illegitimate name *Squamataxus* for *Saxegothaea*, Nelson (1866: 168) emphasized the similarities of likeness of their bracteose strobili with the fleshy ones in *Taxus* L. By taking into account these differences, it is proposed that Saxegothaeaceae be maintained apart from the other families of Podocarpales Pulle *ex* Reveal (Pherosphaeraceae [Pilg.] Nakai, Podocarpaceae Endl., Nageiaceae Fu, and the recently established Acmopylaceae Bobr. & Melik.) by placing them in their own order, Saxegothaeales. The recognition of Saxegothaeaceae brings into question the relationship of the arborescent Chilean genus *Saxegothaea* with the shrubby Tasmanian genus *Microcachrys*. In addition to their distinct habit, the several morphological differences in their reproductive structures (Morvan 1990) and the numerous differences in their vegetative features leads us to establish a new monogeneric family, Microcachrydaceae, for the isolated endemic. We hereby assign Microcachrydaceae to the Saxegothaeales.

Taxopsida R. Florin & Doweld et Reveal, *class. nov.* TYPUS: *Taxus* L., *Sp. Pl.* 2:1040. 1753.; Taxaceae Gray, *Nat. Arr. Brit. Pl.* 2:222, 226. 1821., *nom. cons.*

Ab classis Pinopsida habitum fruticibus vel arbusculis ramosissimis, lignum pycnoxylicum resiniferum, tracheidas spirales tertiarias, lepides nullae, 'stamina' squamata peltataque, microsporangiis 2-8, uniloculaanbus, grana pollinis asaccata, ovula solitaria vel cum brachyblasto squamoso, semina

drupacea, erecta in conos squamosos conferta, arillo bracteisve adnata, embryonibus dicotyledoneis differt.

Podocarpopsida Doweld & Reveal, *class. nov.* TYPUS: *Podocarpus* L'Hér. *ex* Pers., *Syn. Pl.* 2:580. 1807., *nom. cons.*; Podocarpaceae Endl., *Syn. Conif.* 203. 1847., *nom. cons.*

Ab classis Pinopsida habitum fruticibus ramosis vel rario arboribus, foliis spiraliter dispositis, vel planis latisque, lanceolatis vel ovoideis, nervatione parallela, interdum phyllocladiis; conos lignescentes nullos, strobilis femineis in aggregationes oligomeras vel rarius polymeras confertis; ovula erecta vel plerumque inversa, epimatio cincta vel varie connata (raro nullo: Pherosphaeraceae); semina singula in axillis megasporophyllorum strobilarium disposita differt.

Saxegothaeales Doweld & Reveal, *ord. nov.* TYPUS: *Saxe-Gothaea* Lindl., J. Hort. Soc. London 6:258. 1851.; Saxegothaeaceae Gaussen *ex* Doweld et Reveal, Phytologia 84:365. 1999.

Arbores vel frutices; folia plana, acicularia, spiraliter disposita vel squamiformia, decussata; strobili masculi amentiformes, microsporangia 2; strobili feminei polyspermi, squamosi; semina inversa, epimatio membranaceo bilaterali cincta.

Saxegothaeaceae Gaussen *ex* Doweld & Reveal, *fam. nov.* TYPUS: *Saxe-Gothaea* Lindl., J. Hort. Soc. London 6:258. 1851.

Arbores sempervirentes, monoicae; rami patentes, subverticillati; folia sparsa, linearia, plana, cum nervo longitudinali minuto, basi fere in petiolum brevem angustata; strobilis masculis bracteae microsporangiferae dilatato-acuminatae, microsporangia 2, unilocularia, longitudinaliter dehiscentia; strobili feminei amentiformes subcapitati, bracteae plures, lanceolatae, inferne connatae, inferiores et supremae steriles, fertiles 1-2, monospermae; semen inversum, epimatio non connatum (cinctum).

Microcachrydaceae Doweld & Reveal, *fam. nov.* TYPUS: *Microcachrys* Hook.*f.*, London J. Bot. 4:149. 1845.

Frutices dioici, prostrati, ramosi, ramulis e foliis arcte imbricatis tetragonis; strobili masculi in amenta ovali-oblonga conferti, bracteae microsporangiferae ovato-orbiculatae; microsporangia 2, stipitulata, connectivo curvato ultra loculos producto; strobili feminei amentiformes, bracteae arcte imbricatae ovato-rhomboideae; megasporophyllum succulentum; semina minutissima ovoidea, epimatio bilaterali a basi ad medium cincta (non connata).

In order to maintain coordinate ranks among the Pinophyta, the following name is required.

Podocarpidae Doweld & Reveal, *subcl. nov.*, validated by a full and direct reference to the Latin description associated with a validly published Endlicher (*Syn. Conif.* 203. Mai-Jun 1847, as Podocarpaceae ["Podocarpeae"]) family name. TYPUS: *Podocarpus* L'Hér. *ex* Pers., *Syn. Pl.* 2:580. 1807., *nom. cons.*; Podocarpaceae Endl., *Syn. Conif.* 203. 1847., *nom. cons.*

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TRANSFER OF SOME SPECIES FROM *GILIA* TO *ALLOPHYLLUM* AND *TINTINABULUM*, AND THE EFFECTS OF THE TRANSFER ON THE GENERIC DEFINITION OF *GILIA* (POLEMONIACEAE)

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ABSTRACT

Three species of *Gilia* are transferred to *Allophyllum* and one to *Tintinabulum*. The transfers are supported by pollen morphology as well as by type of vestiture and various gross morphological characters. *Allophyllum* now has an expanded range of variation with two sections, *Allophyllum* sect. *Allophyllum* and *A*. sect. ***Kelloggia***, *comb. nov.* The small genus *Tintinabulum* now has four species including ***T. tenerrimum***, *comb. nov.* The exclusions make *Gilia* more natural than it has been in many decades. The tribe Gilieae has also become more natural or monophyletic as a result of the present and other recent transfers. Pollen aperture arrangement turns out to be a very good taxonomic character in the Polemoniaceae. The *Gilia* tribe is zonocolporate with rare exceptions, while the other tribes with rare exceptions are pantoporate. The approach of molecular cladistics to classification of Polemoniaceae is critiqued.

KEY WORDS: *Gilia, Allophyllum, Tintinabulum, Aliciella*, Polemoniaceae, pollen morphology, phylogeny

This paper deals with the relationships of four species of western montane annual herbs which have long been treated as members of *Gilia*. Three of the species--*G. leptalea* (A. Gray) Greene, *G. capillaris* Kellogg, and *G. sinistra* M.E. Jones--currently form the section *Kelloggia* of *Gilia* (Day 1993a, 1993b; Grant 1999). The fourth species is the *G. tenerrima* A. Gray of floras and manuals.

On external morphology, the four species appear to belong in *Gilia*. However, certain microscopic characters have forced a reconsideration of their relationships. In pollen characters, section *Kelloggia* differs from the rest of *Gilia*, but agrees with *Allophyllum*. The four species possess a type of glandular hair that is found in *Allophyllum* and *Tintinabulum*, but not in the rest of *Gilia*. There are also some gross morphological characters that differentiate the four species from *Gilia* proper.

The character relationships suggest that the four species should be taken out of *Gilia*, that section *Kelloggia* should be placed in *Allophyllum*, and that *G. tenerrima* A. Gray belongs in *Tintinabulum*. Here we present the evidence for the proposed transfers and make the formal taxonomic and nomenclatural changes. The effects of the changes on the definition of the genera *Allophyllum* and *Gilia* and the tribe Gilieae are discussed.

We will sometimes refer to the species involved as gilias, sometimes as allophyllums or tintinabulums, depending on the historical context. When referring to a given species as it was in the past, we cite it as a *Gilia*, but it is cited as an *Allophyllum* or *Tintinabulum* when looking to the future. The term "true gilias" is used for the genus *Gilia* exclusive of section *Kelloggia* and *G. tenerrima* A. Gray. The original members of *Allophyllum* will be referred to as the "typical allophyllums" or *Allophyllum* sect. *Allophyllum*.

CHARACTERS

Pollen morphology.

Good surveys of the various morphological features of the pollen grains in the family Polemoniaceae as a whole were made by Stuchlik (1967a, 1967b) and Taylor & Levin (1975). Additional observations in particular genera have been recorded for *Collomia, Acanthogilia*, and *Maculigilia* (Chuang *et al.* 1978; Day & Moran 1986; Patterson 1989). *Maculigilia* is a new monotypic genus recently segregated from *Gilia* (Grant 1999). Day investigated pollen morphology in *Gilia* proper, *G. tenerrima* A. Gray, and *Allophyllum*, and the new results are presented here (Table 1, Figure 1).

Because there are numerous palynological characters varying among numerous polemon genera and species, authors have sought to reduce this variation to a manageable number of syndromes or "types" (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Chuang *et al.* 1978). This has its advantages, but also disadvantages. Important single characters become lost in the aggregate syndrome.

The location of the apertures on the pollen grain is one such character. We have singled it out and found it to be a very useful indicator of relationships. Two contrasting conditions are: pantoporate (apertures scattered over grain) and zonocolporate (apertures located in the equatorial zone).

In all sections of the true gilias, the pollen is zonocolporate. In the original or typical allophyllums, by contrast, it is pantoporate. In the three species of section *Kelloggia*, it is also pantoporate (Table 1, Figure 1).

Table 1. Several characters of the pollen grains (pore location and exine pattern) in typical *Allophyllum* and some former members of *Gilia*. From Stuchlik (1967a), Taylor & Levin (1975), and Day (herein).

Allophyllum gilioides (Bentham) A.D. Grant & V. Grant. Pantoporate; pertectate, spinulose. California. *Ellison, s.n.* (Stuchlik).

A. gilioides (Bentham) A.D. Grant & V. Grant subsp. *gilioides*. Pantoporate; pertectate, spinulose. California. *Hoover 3003.* (Taylor & Levin).

A. gilioides (Bentham) A.D. Grant & V. Grant subsp. *violaceum* (Heller) A.G. Day. Pantoporate; pertectate, spinulose. Lake Almanor, Plumas Co., CA. *Taylor 4639.* (Day).

A. divaricatum (Nuttall) A.D. Grant & V. Grant. Pantoporate; pertectate, spinulose. Twain Harte, Tuolumne Co., CA. *V. Grant & A.D. Grant 9449.* Figure 1A. (Day).

Gilia sinistra M.E. Jones subsp. *sinistra*. Pantoporate; pertectate, spinulose. Blue Mts., Asotin Co, WA. *Cronquist 5915.* Originally reported as *G. capillaris* Kellogg, but specimen reidentified as above. (Stuchlik).

G. sinistra M.E. Jones subsp. *sinistra*. Pantoporate, pertectate, spinulose. Sagehen Creek, Nevada Co., CA. *Day & Trewbridge 83-74.* Figure 1B. (Day).

G. sinistra M.E. Jones subsp. *pinnatisecta* (Mason & A. Grant) Day. Weaverville, Trinity Co., CA. *Day & Robinson 84-19.* (Day).

G. capillaris Kellogg. Pantoporate; striate. Holcomb Valley, San Bernardino Mts., s. CA. *A.G. Day 62-20.* (Day).

G. leptalea (A. Gray) Greene subsp. *leptalea*. Pantoporate; striate. Butte Meadows, Butte Co., CA. *Heller 12817.* (Taylor & Levin). Note: the authors report zonocolporate pollen in their description, but their photograph shows it to be pantoporate.

G. leptalea (A. Gray) Greene subsp. *bicolor* Mason & A.D. Grant. Pantoporate; striate. Sagehen Creek, Nevada Co., CA. A.G. Day 82-100. Figure 1C. (Day).

G. leptalea subsp. *bicolor*. Pantoporate; striate. Slate Creek Valley, Mono Co., CA. *Clausen 1962.* (Day).

G. filiformis Parry ex A. Gray. Zonocolporate; striate. California. *Craig 843.* (Stuchlik).

G. tenerrima A. Gray. Zonocolporate, with numerous closely-spaced colpi, ± equatorial in position, but the equatorial band sometimes modified into a figure-of-8 form; exine striate. Bodie Hills near Masonic Mt., Mono Co., CA. *Lavin SW31b.* (Day).

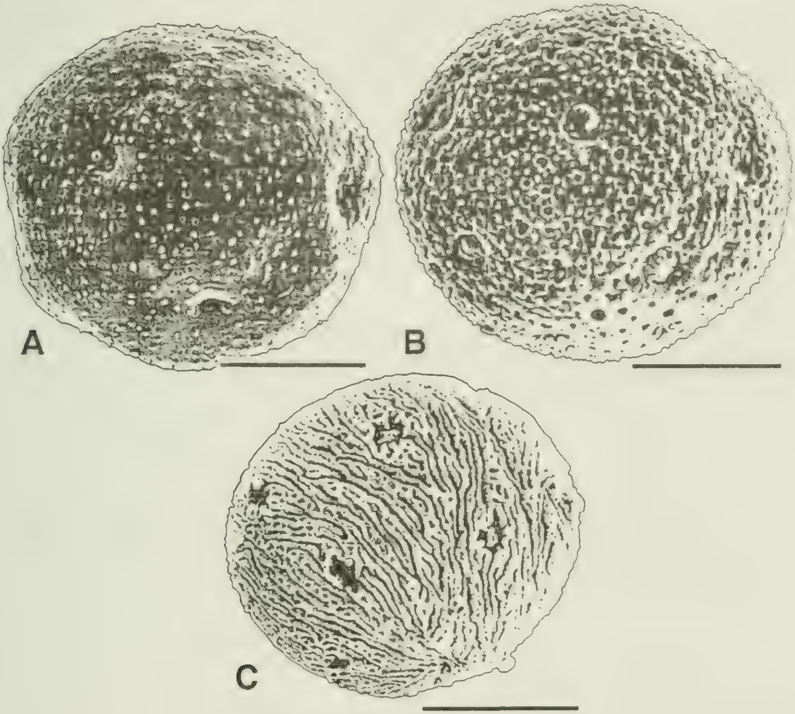

Figure 1. Pollen grains of Allophyllum and Gilia sect. Kelloggia. (A) Allophyllum divaricatum (Nuttall) A. Grant & V. Grant; Twaine Harte, Tuolumne Co., CA. (B) Gilia sinistra M.E. Jones ssp. sinistra; Sagehen Creek, Nevada Co., CA. (C) Gilia leptalea (Gray) Greene ssp. bicolor Mason & A. Grant, Slate Creek Valley, Mono Co., CA. Collection numbers in Table 1. Drawn from SEM photos of Day. Scale line 15 microns.

Next, consider the exine pattern. In *Gilia* exclusive of *Kelloggia*, the pattern varies but is commonly striate. In *Allophyllum* sect. *Allophyllum*, the exine has spinules. *Gilia sinistra* has a spinulose exine like typical *Allophyllum*. However, the exine is striate in *Gilia capillaris* and *G. leptalea* (Table 1, Figure 1). Thus, the exine pattern varies among species in *Kelloggia*, but exhibits the typical *Allophyllum* condition in one of the species.

Gilia tenerrima has zonocolporate striate pollen, as does *G. filiformis* Parry *ex* A. Gray (Table 1). The pore arrangement in *G. tenerrima* is unusual, which led to its being misinterpreted as "approaching pantoporate" in a previous paper (Grant 1999). A better characterization is broad-banded zonocolporate (see Table 1).

Trichomes.

The true gilias and *Allophyllum* sect. *Allophyllum* both have stipitate glandular hairs on the upper stems and often in the inflorescence. These trichomes consist of a chain-like series of cells forming a stalk and a terminal globular single-celled sticky gland. In the species of true gilias that have been examined, the stalk is generally stout and the terminal gland is usually amber-colored. In typical *Allophyllum*, the stalk is long, slender, and translucent, and the terminal gland is a black dot (Figure 2).

The latter type of glandular hair is unusual in the temperate genera, but is found again in a modified form in *Kelloggia*. The glandular hairs of *Kelloggia* are greatly reduced in size as compared with typical *Allophyllum*. They often have a short single-celled stalk, in which case they measure ca. 0.05 mm long. The terminal gland is a black dot as in typical *Allophyllum* (Figure 2).

The glandular hairs of *Gilia tenerrima* are also of the *Allophyllum* type, with a slender hyaline stalk bearing a black dot-like gland. They are tiny as in *Kelloggia*, measuring 0.07-0.13 mm long. We at first construed this as evidence for a relationship of *G. tenerrima* with *Allophyllum* sect. *Kelloggia*, but then we discovered the same type of tiny black-tipped gland in *Tintinabulum inyoensis* (I.M. Johnston) V. Grant, which *G. tenerrima* resembles in gross morphological characters.

Other Characters.

Seed form and color are conservative characters in the temperate Polemoniaceae, and are good indicators of generic and tribal relationships (Grant 1998). The true gilias and *Allophyllum* sect. *Allophyllum* differ with respect to these seed characters. In true gilias, the seeds are small, angular, and sandy colored. In typical *Allophyllum*, they are large, plump, with a rounded contour on one side at least, and brown or black. It is significant that mature seeds of *Kelloggia* are also plump, rounded and dark brown, as in typical *Allophyllum*.

To summarize, the three species of *Kelloggia* differ from the rest of *Gilia*, but agree with *Allophyllum* sect. *Allophyllum* in pollen pore arrangement, type of trichome, and seed characters. In addition, one species of *Kelloggia* is like the typical allophyllums in pollen exine pattern.

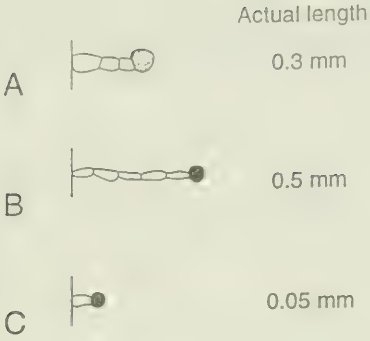

Figure 2. Types of stipitate glandular hairs. Hairs shown as attached to side of upper stem or pedicel. The terminal gland is amber-colored in A, and black in B and C. (A) *Gilia capitata* Sims ssp. *pacifica* V. Grant; Mendocino Co. coast. (B) *Allophyllum violaceum* (Heller) A. Grant and V. Grant; southern Sierra Nevada, Kern Co. (C) *Gilia leptalea* (Gray) Greene; central Sierra Nevada, Sierra Co. All localities in California. A and B to same scale, C drawn at a much higher magnification than A and B.

Gilia tenerrima has a growth habit of spreading branches with slender stems, and the flowers are usually solitary. In these respects it differs from *Gilia* proper but is like *Tintinabulum*. The corolla is small and campanulate in both *G. tenerrima* and *Tintinabulum*. As noted earlier, tiny black-tipped glandular hairs occur in both *G. tenerrima* and *Tintinabulum inyoensis*.

The DNA evidence published to date for *Kelloggia* is scanty. It consists of the sequence in the cpDNA gene matK in *Gilia sinistra* (Johnson *et al.* 1996). In the cladogram for this gene, *G. sinistra* falls in a clade of *Navarretia* species (Johnson *et al.* 1996). *Gilia sinistra* is remote from *Navarretia* by nonmolecular criteria of relationships. More molecular work on *Kelloggia* is desirable.

In the cpDNA and nrDNA cladograms (Johnson *et al.* 1996; Porter 1997), *Gilia tenerrima* falls close to the far-western annual gilias (*Gilia* subgen. *Gilia*), but is remote from *G. filiformis*. This is one of the unexplained cases of discordance between molecular and morphological data in the family.

THE EXPANDED GENUS *ALLOPHYLLUM*

Allophyllum is a small genus related to *Collomia* in the tribe Polemonieae. It was set up in 1955 for the former *Gilia gilioides* (Bentham) Greene group (Grant & Grant 1955). The group consists of four or five species depending on how one treats the taxa *gilioides* and *violaceum*. These entities behave as distinct sympatric species in some parts of their range (Grant & Grant 1955) and as intergrading races in other areas (Day 1993b, unpubl.). Accordingly, one can treat them either as separate species (Grant & Grant 1955) or as two subspecies of one species (Day 1993a, 1993b). We will treat them as one polytypic species in this paper.

The transfer of the *Gilia leptalea* group to *Allophyllum* introduces a distinctive element into the genus and expands its range of variation. The relationships between the old allophyllums and the new *A. leptaleum* (A. Gray) A. Day & V. Grant group can be expressed taxonomically by treating them as separate sections.

The revised classification of *Allophyllum* is presented in outline form. Diagnoses are given rather than descriptions. The essential nomenclature is presented rather than complete synonymy. For more details see the treatments of Grant & Grant (1955) and Day (1993a).

ALLOPHYLLUM (Nuttall) A. Grant & V. Grant, Aliso 3:98. 1955. TYPE SPECIES: *Gilia divaricata* Nuttall. BASIONYM: *Gilia* sect. *Allophyllum* Nuttall, J. Acad. Nat. Sci. Philadelphia, ser. 2 1:155. 1848.

Annual herbs with leafy stems. Plants medium-sized to small. Leaves digitately lobed or simple and entire. Pubescence of glandular hairs consisting of slender translucent stalks and small black tips. Calyx with herbaceous lobes and membranous sinuses. Corolla funnelform, medium-sized to small. Pollen pantoporate. Capsule spherical, dehiscing from top to bottom, and the valves generally falling off. Seeds plump, rounded on one side, brown or black, mucilaginous when wet. Basic chromosome numbers $X = 9,8$.

Western North America, mainly in the Pacific states, but extending into interior western states. Seven (or eight) species in two sections.

ALLOPHYLLUM sect. *ALLOPHYLLUM*

Leaves digitately lobed with an elliptical terminal lobe and 2-5 smaller lateral lobes; tips of lobes blunt and thickened. Glandular hairs relatively large in comparison with section *Kelloggia*. Flowers generally in clusters. Corolla generally concolored. Pollen exine spinulose. Seeds black or brown. Basic chromosome numbers, $X = 9,8$.

Allophyllum divaricatum (Nuttall) A. Grant & V. Grant, *A. integrifolium* (Brand) A. Grant & V. Grant, *A. glutinosum* (Bentham) A. Grant & V. Grant, *A. gilioides* (Bentham) A. Grant & V. Grant subsp. *gilioides*, and *A. gilioides* subsp. *violaceum* (Heller) A.G. Day. Mostly at lower and middle elevations but ranging to higher elevations in mountains.

ALLOPHYLLUM sect. ***KELLOGGIA*** (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* TYPE SPECIES: *Gilia capillaris* Kellogg. BASIONYM: *Gilia* subgen. *Kelloggia* Mason & A. Grant, Madroño 9:219. 1948. *Gilia* sect. *Kelloggia* A. Day, Novon 3:332. 1993.

Leaves mostly linear and unlobed, sometimes bilobed in *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant; leaf tips sharp-pointed in *A. leptaleum* (A. Gray) A. Day & V. Grant and *A. capillare* (Kellogg) A. Day & V. Grant, but blunt in *A. sinistrum*. Glandular hairs tiny compared with those in section *Allophyllum*. Flowers solitary in upper leaf axils. Corolla concolored, bicolored or tricolored, showy or small. Pollen exine spinulose in *A. sinistrum*, but striate in the other two species. Seeds dark brown at maturity. Basic chromosome number, $X = 9$.

Three species as listed below.

1. ***Allophyllum capillare*** (Kellogg) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia capillaris* Kellogg, Proc. California Acad. Sci. 5:46. 1873.

   Mountains from southern Oregon to southern California, east to Idaho; rare in Utah. Occurs sympatrically with *Allophyllum sinistrum*.

2. ***Allophyllum leptaleum*** (A. Gray) A. Day & V. Grant, *comb. nov.* BASIONYM: *Collomia leptalea* A. Gray, Proc. Amer. Acad. Arts 8:261. 1870. *Gilia leptalea* Greene, Erythea 4:58. 1896.

   Cascade Mountains of Oregon to southern Sierra Nevada of California.

2a. *Allophyllum leptaleum* (A. Gray) A. Day & V. Grant subsp. *leptaleum.*

Wide ranging.

2b. ***Allophyllum leptaleum*** (A. Gray) A. Day & V. Grant subsp. ***bicolor*** (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia leptalea* (A. Gray) Greene subsp. *bicolor* Mason & A. Grant, Madroño 9:220. 1948.

High Sierra Nevada in Mono County, California.

3. ***Allophyllum sinistrum*** (M.E. Jones) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia sinistra* M.E. Jones, Contrib. West. Bot. 10:57. 1902.

Mountains from southern Washington to southern California, east to Nevada; rare in Colorado.

3a. *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant subsp. *sinistrum.*

Wide ranging.

3b. ***Allophyllum sinistrum*** (M.E. Jones) A. Day & V. Grant subsp. ***pinnatisectum*** (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia leptalea* (A. Gray) Greene subsp. *pinnatisecta* Mason & A. Grant, Madroño 9:220. 1948. *Gilia sinistra* M.E. Jones subsp. *pinnatisecta* A. Day, Novon 3(4):332. 1993.

North Coast Ranges, California.

TINTINABULUM TENERRIMUM

In a previous paper (Grant 1999), a small species group consisting of *Gilia campanulata* A. Gray, *G. filiformis* Parry *ex* A. Gray, and *G. inyoensis* I.M. Johnston was excluded from *Gilia*. The long dormant genus *Tintinabulum* of Rydberg (1917) was revived to accommodate them. A modern characterization of *Tintinabulum* has been given recently (Grant 1999) and does not need to be repeated here. *Tintinabulum* was assigned to the tribe Gilieae.

In the same paper (Grant 1999), *Gilia tenerrima* A. Gray was transferred to *Allophyllum*. This change was based on the finding of several *Allophyllum*-like characters in *G. tenerrima*: namely, rounded brown seeds, tiny black-tipped glands, a type of leaf lobing and capsule dehiscence, and what was thought to be semi-pantoporate pollen. Since then it has been found that the pollen of *G. tenerrima* is atypical zonocolporate (Table 1) and that tiny black-tipped glands occur in *Tintinabulum inyoensis* (I.M. Johnston) V. Grant as well as in *Allophyllum*. These findings weaken the case for an *Allophyllum* relationship.

Gilia tenerrima shares a number of distinctive vegetative and floral characters in common with *Tintinabulum*: spreading growth habit, slender stems, solitary flowers, campanulate corollas. These character similarities indicate a relationship. *Gilia tenerrima* was grouped with the *G. campanulata* alliance in two previous treatments (Mason & Grant 1951; Day 1993a), and, after a brief stay in *Allophyllum*, is now returned to that alliance.

Tintinabulum tenerrimum (A. Gray) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia tenerrima* A. Gray, Proc. Amer. Acad. Arts 8:277. 1870. *Navarretia tenerrima* Kuntze, *Rev. Gen. Pl.* 2:433. 1891. *Allophyllum tenerrimum* V. Grant, Phytologia 84:79. (1998) 1999.

DISCUSSION

Progress in the Delineation of *Gilia*

At the turn of the last century the genus *Gilia* was a collection of distantly related subgroups, many of which were closer to other genera than they were to the core sections of *Gilia*. The genus was highly polyphyletic. The genus problem facing botanists was to identify the monophyletic subgroups that were contributing to the polyphyly of *Gilia* and to segregate them out into other genera.

The process of moving unrelated subgroups out of *Gilia* was begun early in the 20th century by Milliken (1904), who set up the segregate genus *Navarretia*, and transferred *Gilia maculata* Parish to *Linanthus*. The process was continued by a succession of later botanists. By the time of the general treatment of *Gilia* of Grant (1959), most of the large extraneous subgroups had been placed elsewhere in the system, and *Gilia* had become a fairly natural genus.

But some extraneous species and small species groups still remained in *Gilia* in 1959. Moran (1977) transferred *Gilia uncialis* Brandegee to *Linanthus*. More recently, Grant (1999) excluded *G. tenerrima* A. Gray from *Gilia*, and moved the small *G. campanulata* A. Gray group into the resurrected genus *Tintinabulum*. The transfer here of the *G. leptalea* (A. Gray) Greene group to *Allophyllum* is in line with the earlier moves. It is interesting that no transfers from other genera into *Gilia* have been made in modern times.

Gilia is now more natural that it has been in the past. A putative phylogenetic tree of the genus based on all available taxonomic characters, conventional and unconventional, is shown in Figure 3. The subgenera and sections of *Gilia* are linked together by shared conservative characters in seeds, pollen, and basic chromosome number, and by various less conservative characters in leaves, pubescence, calyx, and corolla (see Grant 1998, 1999).

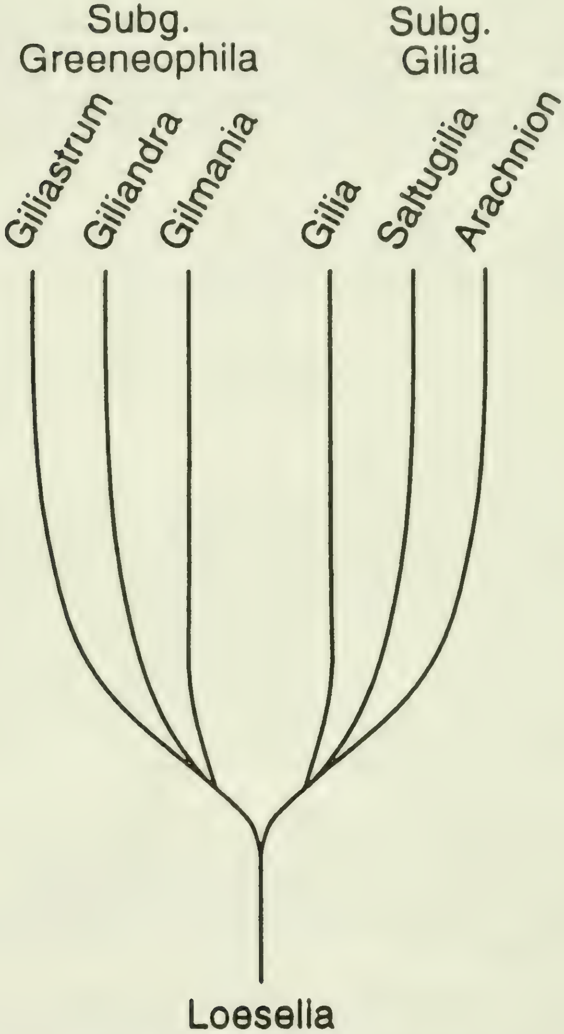

Figure 3. The subgenera and sections of Gilia after the transfers made here, and the proposed phylogenetic relationships of these subgroups.

Comments on the Segregation of the Genus *Aliciella*

The splitting off of subgroups as segregate genera can go too far. Where should we draw the line? Segregating subgroups out of a genus in order to reduce polyphyly is one thing: splitting the branches of a single monophyletic group into separate genera is something else. The first action is necessary for phylogenetic taxonomy; the latter type of change is unnecessary from a phylogenetic standpoint. Furthermore, the splitting up of a heterogenous, but monophyletic genus into two or more separate genera is generally undesirable taxonomically since it obscures the relationship between the branches.

Porter (1998a) has recently segregated the genus *Aliciella* from *Gilia* proper. *Aliciella* sensu Porter corresponds to *Gilia* sects. *Giliandra* and *Gilmania* (Figure 3; Grant 1999). In a second paper, Porter (1998b) elevates the section *Giliastrum* of *Gilia* to a separate genus. Porter's stated reason for the changes made in both papers is to reduce polyphyly in *Gilia*. Thus, Porter has the same goal as we do, but arrives at a very different result.

Porter is an exponent of molecular cladistics, whereas our work is carried out in the framework of traditional taxonomy and evolutionary systematics. The two approaches are very different, and they lead to disagreement regarding phylogenetic classification of *Gilia*. Molecular cladistics emphasizes the diagnostic value of single DNA segments, and it processes the DNA evidence by the procedures of cladistics to produce cladograms. The cladograms are often misconstrued in practice as organismic phylogenies (see Grant 1998). Traditional and evolutionary systematists have learned from long experience to beware of overemphasis on any single character; we stress the importance of using all available characters to construct classifications and infer phylogenies. The best use of DNA evidence in systematics, in our opinion, is to integrate it with all other types of evidence, rather than to overgeneralize from a molecular cladogram (Turner 1998; Grant 1998).

Porter's (1998a) segregation of *Aliciella* from *Gilia* is based primarily on the molecular cladogram for nrDNA ITS (Porter 1997). Supplementary evidence comes from Johnson *et al.*'s (1996) work on the cpDNA gene matK, but these authors assayed only three of the twenty species belonging to *Aliciella* sensu Porter. Porter (1998a) cites other lines of molecular and morphological evidence (Porter 1993; Tommerup & Porter 1996). However, the role of this supplementary evidence is difficult to assess since it is unpublished (as of this writing), one reference being a dissertation and the other a lecture abstract, and the data are not summarized in the 1998 paper. Porter (1998a) does give detailed morphological descriptions of the species; but he does not present parallel short diagnoses of the main groups involved, which would be more helpful than descriptions in revealing the morphological characters used in the classification.

In addition to setting up *Aliciella* as a genus, Porter recognizes three levels of infrageneric groups; subgenera, sections, and subsections. Each one of these groups from genus to subsection is defined in cladistic terms. Here is the definition of section *Giliandra* of *Aliciella*. "Section *Giliandra* is phylogenetically defined as the most recent common ancestor of *Aliciella pinnatifida* and *A. stenothyrsa* and all of the descendants of that ancestor." (Porter 1998a, p. 27.). Parallel definitions are given for the other main groups. Thus, the groups are clades, or cladons in the terminology of Mayr (1995) and Brummitt (1997). The only cladograms published for the *Gilia-Aliciella* group are molecular cladograms. The separation of *Aliciella* from *Gilia* subgen. *Gilia* is in agreement with the cpDNA and nrDNA cladograms, and the subdivisions of *Aliciella* correspond with the clades and subclades in the nrDNA cladogram (Porter 1997, 1998a).

But the molecular cladograms are gene trees, not organismic phylogenies. Furthermore, they can be interpreted in different ways. The cladograms are consistent with the view that *Gilia* sect. *Giliandra* and *Gilmania* (or *Aliciella*) are only distantly related to *Gilia* subgen. *Gilia*. This agrees with the prevailing view based on morphological evidence. But is does not necessarily follow that the branches involved should be separated at the genus level. For generic segregation, more evidence and stronger arguments are needed than those presented by Porter (1998a).

In another paper, Porter (1998b) takes the first step in segregating *Gilia* sect. *Giliastrum* as a genus. This short paper makes the nomenclatural changes of the species involved; it contains little discussion and our discussion will be brief. Here again, as in the case of *Aliciella*, the main evidence is the cpDNA and nrDNA cladograms of Johnson *et al.* (1996) and Porter (1997), along with other unpublished molecular studies of Porter. It appears that another big taxonomic change is being made on a narrow data base, and without considering the difference between segregation for the sake of monophyly and splitting for the sake of homogeneity.

Improved Definition of the Tribe Gilieae

The transfer of section *Kelloggia* from *Gilia* to *Allophyllum* reduced the polyphyly in the tribe Gilieae as well as that in the genus *Gilia*. It is the latest in a series of transfers that have made the *Gilia* tribe more natural. To see this in perspective, it is necessary to go back in time. When the Gilieae was set up years ago, it consisted of seven genera in three or four groups: namely, the basal genus *Gilia*; *Ipomopsis-Eriastrum-Langloisia*; *Navarretia*; and *Leptodactylon-Linanthus* (Grant 1959, p. 258). This assemblage was believed to be phylogenetically natural at that time, according to the evidence then available, but new evidence in subsequent years brought cases of unnaturalness to light, and a series of taxa were excluded from the tribe.

The species formerly known as *Ipomopsis gloriosa* (Brandegee) A. Grant was segregated into the new genus *Acanthogilia* (Day & Moran 1986), and this was placed in a tribe of its own (Grant 1998). *Leptodactylon* and *Linanthus* were removed to a new tribe Leptodactyloneae on the basis of a combination of molecular and morphological characters (Grant 1998). *Navarretia* was transferred to the tribe Polemonieae on combined molecular and morphological evidence (Grant 1998). The former *Gilia maculata* Parish was placed in a new genus (*Maculigilia*) in the Leptodactyloneae (Grant 1999). The transfer of *Gilia* sect. *Kelloggia* to *Allophyllum* in this paper continues the process.

The reduced tribe Gilieae, consisting now (in our system) of *Gilia, Ipomopsis, Eriastrum, Langloisia*, and the resurrected genus *Tintinabulum*, is much more natural than it was. Common characters in the seeds, calyx, leaves, and ecology help to define it. To these is added unexpectedly a pollen character.

The pollen is pantoporate in the tropical and subtropical genera of the Polemoniaceae and in the temperate tribe Leptodactyloneae (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Day & Moran 1986; Day unpubl.). It is pantoporate throughout the tribe Polemonieae with the exception of some species of *Collomia* which have zonocolporate pollen (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Chuang *et al.* 1978; Day unpubl.). By contract, the pollen is zonocolporate throughout the tribe Gilieae as presently delimited with the exception of some pantoporate species of Eriastrum (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Day unpubl.).

Taylor & Levin (1975) related pollen characters to phylogenetic relationships in the Polemoniaceae as these two variables were understood at that time. They suggested that the zonocolporate condition was ancestral and the pantoporate condition was derived in the family (*op. cit.*, p. 110). We have more information about pollen characters and a better system of classification today. The systematic distribution of pore arrangement as we now know it, clearly indicates that the pantoporate condition is ancestral, that the zonocolporate condition is derived, and that a zonocolporate character state is definitive of the *Gilia* tribe with only a few exceptions.

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NOTE ADDED IN PROOF

The present composition of the tribe Gilieae as outlined above needs to be qualified. The five genera listed are the extant members of the tribe. Lott *et al.* (1998) have recently discovered and described a mid-Eocene genus, *Gilisenium*, which belongs in the Gilieae and is close to *Gilia*. This important discovery shows that the tribe is much older than we and others have thought.

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Phytologia (May 1998) 84(5):384.

NEW NAMES IN THIS ISSUE OF PHYTOLOGIA

As a result of the International Botanical Congress in Tokyo in 1993, the International Association of Plant Taxonomy has been tasked with exploring the feasibility of registration of plant and fungi names. In accordance with terms of the pilot implementation of the registration concept, new names and combinations produced in this issue of PHYTOLOGIA are listed below.

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